THE JURASSIC AMMONITE BREDYIA BUCKMAN

by J. R. SENIOR

ABSTRACT. The lower Aalenian (Middle Jurassic) ammonite *Bredyia subinsignis* (Oppel, 1856) has been investigated at several growth stages and found to be dimorphic. *Burtonia crassornata* Buckman (1910a), the type species of *Bredyia* Buckman (1910b), is regarded as a junior synonym of *Ammonites subinsignis* Oppel (1856) as are *Hammatoceras newtoni* Buckman (1892), *H. feugeurollense* Brasil (1893), and several species described by Dumortier (1874).

THE lower Aalenian genus *Bredyia* belongs to the Hammatoceratinae, a subfamily of ammonites which, because of their comparative rarity, have not been studied in detail, although numerous references can be found in the literature.

In the Aalenian (Middle Jurassic) of Europe, the ammonite fauna is composed predominantly of leioceratinids, on which the present system of zonation is largely based (Arkell 1956, p. 10); this zonation is under review as a result of fresh field information. In addition to leioceratinids, smaller numbers of tmetoceratinids, lytoceratids, and hammatoceratinids occur, and in areas of Tethyan influence phylloceratids also often constitute a large percentage of the ammonite fauna (text-fig. 1).

Some hammatoceratinids are important since they are probably directly ancestral to two prolific ammonite groups in the Jurassic, the Sonninidae, and the Stephanocerataceae (Arkell 1957, p. L287), and are also probably indirectly ancestral to a third group, the Perisphinctaceae (Spath 1931, p. 279; Arkell 1957, p. L308; Sturani 1971, p. 153). *Bredyia* apparently remained a minor and obscure element in Lower Aalenian faunas.

SYSTEMATIC PALAEONTOLOGY

Family PHYMATOCERATIDAE Hyatt, 1867 Subfamily HAMMATOCERATINAE Buckman, 1887

The Phymatoceratidae have been divided into two subfamilies (Arkell 1957, pp. L265 and L267; ICZN opinion 575, 1959), the ancestral Phymatoceratinae and the Hammatoceratinae. The former is restricted to the Toarcian, but the latter ranges from the Upper Toarcian to the Lower Bajocian. Before 1960 little had been written about the keeled members of the Hammatoceratinae, but since then several authors have figured and described faunas containing them. In describing ammonite faunas from the Bassin Rhodanien, Elmi (1963) used much of the generic nomenclature erected by Buckman (1919–1928) for the keeled hammatoceratinids and also described a new genus, *Pseudanmatoceras* and a new subgenus *Rhodaniceras*. Géczy (1966), however, working independently on faunas from the Mount Bakony area of Hungary, recognized only two genera within the Hammatoceratinae, *Euaptetoceras* and

SCISSUM ZONE	LEIOCERATINAE	HAMMATOCERATINAE	TMETOCERATINAE	LYTOCERATIDAE	PHYLLOCERATIDAE	TOTAL NUMBERS
Burton Cliff, Dorset	70.19% (73)	11.53%	14.42% (15)	3.85%	0% (0)	104
Bonscombe Hill, near Shipton Gorge, Dorset	76.47% (39)	9.80% (5)	9.80%	3.92%	O% (O)	51
Truyas, near Digne, Basses Alpes, France	40, 28% (29)	6.94% (5)	0% (O)	4.17% (3)	48.61% (35)	72
Wochenberg, near Balingen, Württemberg, Germany	96.80% (91)	0% (0)	3.19%	0% (0)	0% (0)	94
OPALINUM ZONE						
Burton Cliff, Dorset	95.58% (238)	0.81%	0.04%	2.03%	0% (0)	246
Green Hill, Innesacre Farm, near Bridport, Dorset	97.01% (65)	1.49%	0% (O)	1.49%	0% (0)	67
Road cutting, Severals, near Crewkerne, Somerset	98.86% (87)	0%	O% (O)	1.14%	O% (O)	88
Heiningen, near Goppingen, Württemberg, Germany	92 .11% (31 5)	0% (O)	0% (O)	7.89% (27)	0% (0)	342

TEXT-FIG. 1. Analysis of cephalopod faunas from the Aalenian of Europe.

Hammatoceras, the latter a genus which Arkell (1957, p. L267) considered to be confined to the Toarcian. In reviewing the work of Elmi and Géczy as well as other literature, Westermann (1969, pp. 63–72) could not '... arrive at any definite opinion regarding the classification of many of the early and intermediate Hammatoceratinae...', but concluded that '... taxonomic levels somewhere midway between the ones reviewed are strongly suggested, similar to the treatment in the Treatise...'. I endorse this moderate view of the suprageneric status of the Hammatoceratinae.

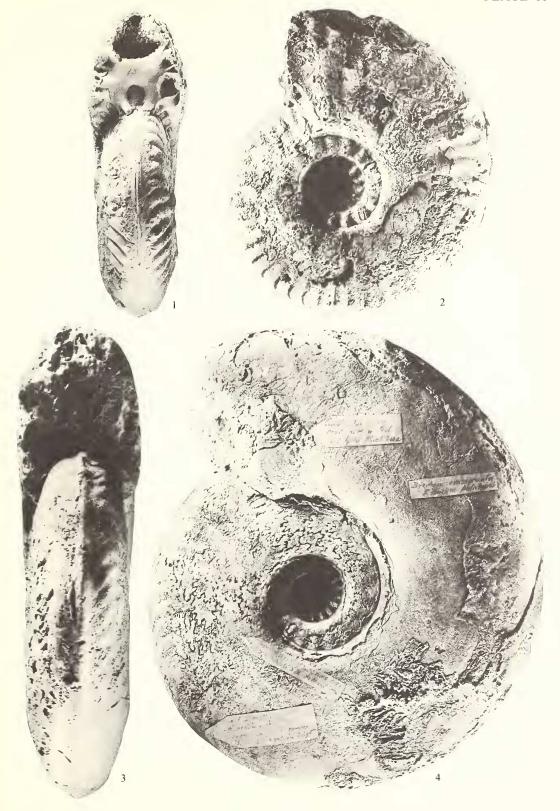
Abbreviations. B—Brigadier G. Bomford Collection (private collection). BM—British Museum (Natural History). GSM—Geological Survey Museum, London. LY—Collection of the University of Lyon, France. MU—University Palaeontological Collection, Munich, West Germany. MM—Manchester Museum. OUM—Oxford University Museum. SH—Department of Geology Collection, University of Sheffield. M—macroconch. m—microconch.

EXPLANATION OF PLATE 81

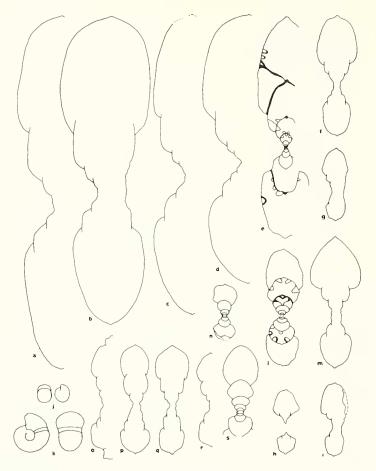
Bredyia subinsignis (Oppel) [M].

Figs. 1, 2. The holotype of *Bredyia crassornata* (Buckman), from the Scissum Beds of Burton Bradstock (probably Burton Cliff), Dorset. Figured by Buckman (1910a, pl. 9, fig. 1) as *Burtonia crassornata*. MM L11221 (Buckman Collection), ×0·44.

Figs. 3, 4. The paratype of *Bredyia crassornata* (Buckman), from the same locality and horizon as figs. 1, 2. Figured by Buckman (1925, pl. DLXXXII). GSM 47763 (Buckman Collection), ×0·5.



SENIOR, Bredyia from the Jurassic of Dorset



TEXT-FIG. 2. Illustrating the ontogeny of *Bredyia subinsignis* (Oppel). a-k, B. subinsignis (Oppel) [M]. a, BM C78467, Scissum Zone, Bonscombe Hill, near Shipton Gorge, Dorset. ×0.5. b, GSM 47763, paratype of B. crassornata (S. Buckman), Scissum Bed, Burton Bradstock, Dorset. × 0·5. c, BM C78462, Scissum Zone, Burton Cliff, Dorset. × 0·5. d, GSM Zx1402, Scissum Zone, Loder's Cross, near Bridport, Dorset. × 0·5. e, BM C78466, Scissum Zone, Bonscombe Hill, Shipton Gorge, Dorset. × 0.5. f and g, figured by Dumortier (1874, pl. 53, figs. 1-4) as Ammonites insignis Zieten. From La Verpilliere, Isère, France. LY 9112 and LY 9118 respectively. × 0·5. h, Munich ASVIII 76, lectotype of A. subinsignis Oppel, Torulosus Schichten, Gomaringen, near Tübingen, Germany. $\times 0.5$. i, LY 9110, holotype of A. alleoni Dumortier (1874, pl. 52, figs. 3, 4), La Verpilliere, Isère, France. × 0·5. j, nucleus showing nepionic constriction and k, protoconch of BM C78465, Scissum Zone, Bonscombe Hill, near Shipton Gorge, Dorset. Both × 14. l, BM C78469 (author's collection), Hammatoceras insigne (Zieten), Upper Toarcian, Leckhampton Hill, near Cheltenham, Gloucestershire. × 0·5. m, LY 9181, H. insigne (Zieten), figured by Dumortier (1874, pl. 54, figs. 4, 5), Upper Toarcian, Saint Nizier, Loire, France. × 0·5. *n*-*s*, *B. subinsignis* (Oppel) [m]. *n*, BM C78461, Scissum Beds, Burton Cliff, Dorset. \times 1. o, GSM 1160HW, Northampton Ironstones, New Duston, near Northampton. \times 1. p and q, BM C78457 and GSM 3666 respectively, Scissum Beds, Burton Cliff, Dorset. $\times 1$. r, BM C77995, Northampton Sands, New Duston, near Northampton. × 1. s, BM C78458, Scissum Beds, Burton Cliff, Dorset. $\times 3$.

Genus Bredyia Buckman, 1910 (Synonym *Pseudammatoceras* Elmi, 1963)

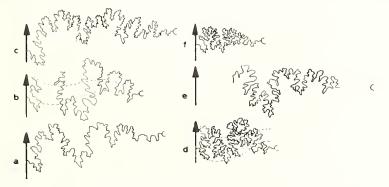
Type species. Burtonia crassornata Buckman, 1910 (= Ammonites subinsignis Oppel, 1856).

Diagnosis. Hammatoceratinid with a massive macroconch which has a small keel and coarse nodate or tuberculate bifurcate ribbing on juvenile whorls, tending to be smooth on the last whorl of the mature shell. Moderately evolute with marked uncoiling of umbilical seam towards maturity. Sutures relatively simple even at larger diameters; the retraction of the umbilical lobe is not marked. Mature apertures are simple and collared. Microconch comparatively small also coarse nodate or tuberculate ribbing continuous up to a mature aperture, which is completed by midlateral lappets. Moderately evolute with no marked excentricity of the umbilical seam towards maturity. Sutures very simple.

Remarks. Although Bredyia is as robust as the ancestral Hammatoceras (text-fig. 2e), the whorl sections are more massive and subquadrate in appearance, only becoming slightly more inflated at maturity in the macroconch; Bredyia [M] is larger and more robust than the macroconchs of the Upper Aalenian genera Planammatoceras and Eudmetoceras.

Ornamentation in *Bredyia* is also distinctive. In *Hammatoceras* the nodate or tuberculate part of the coarse-ribbed ornament (formed where the ribs bifurcate) is very close to the umbilical seam, whereas in *Bredyia* appreciably more of the primaries are seen. At the venter, the secondaries abut almost at right angles to the keel in *Hammatoceras*, but in *Bredyia* the ribs have a definite oral direction at the venter.

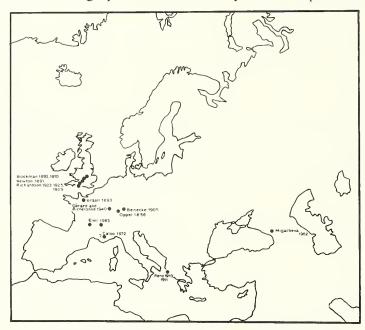
Bredyia differs from the contemporary Erycites which has only a rudimentary keel,



TEXT-FIG. 3. Hammatoceratinid sutures from the Upper Toarcian, Aalenian and Lower Bajocian, all ×0·5. a, paratype of Bredyia crassornata (Buckman) (GSM 47763), suture at 110 mm diameter. Scissum Zone, Lower Aalenian. b, holotype of B. crassornata (Buckman) (MM L11221), suture at 142 mm diameter. Scissum Zone, Lower Aalenian. c, B. subinsignis (Oppel) (OUM J16218), suture at c. 190 mm diameter. Opalinum Zone, Lower Aalenian. d, Hammatocerasinsignis (Zieten) (MM L11290), suture at c. 94 mm diameter. Upper Toarcian. e, holotype of Eudmetoceras amplectens (Buckman) (MM L11287), suture at 168·5 mm diameter. Discites Subzone, Lower Bajocian. f, 'H.' sieboldi (Branco) (Bayer Coll. H20), suture at 69 mm diameter. Murchisonae Zone, Aalenian.

or no keel at all, with ribs which may continue over the venter and a sutural pattern which is very different with a very shallow ventral lobe and first lateral saddle. The degree of simplicity seen in the sutures of *Bredyia* distinguish it from most hammatoceratinids (text-fig. 3) on sutural evidence alone and only the skeletal nature of the second lateral lobe can be used to confirm that this is a hammatoceratinid. In the microconch, because of the small sizes attained at maturity, the sutural appearance is not significantly diagnostic at a generic level.

Distribution. Opalinum Zone in many parts of Europe (text-fig. 4), and more commonly in the Scissum Zone, especially in England. *Bredyia* has also been reported by Westermann (1964, p. 359) from the upper Murchisonae Zone of Beaminster, Dorset, England. However, very extensive collecting at this locality and other localities with exposures of similar stratigraphical horizons has yielded no specimens of *Bredyia*.



TEXT-FIG. 4. The distribution of *Bredyia subinsignis* (Oppel).

EXPLANATION OF PLATE 82

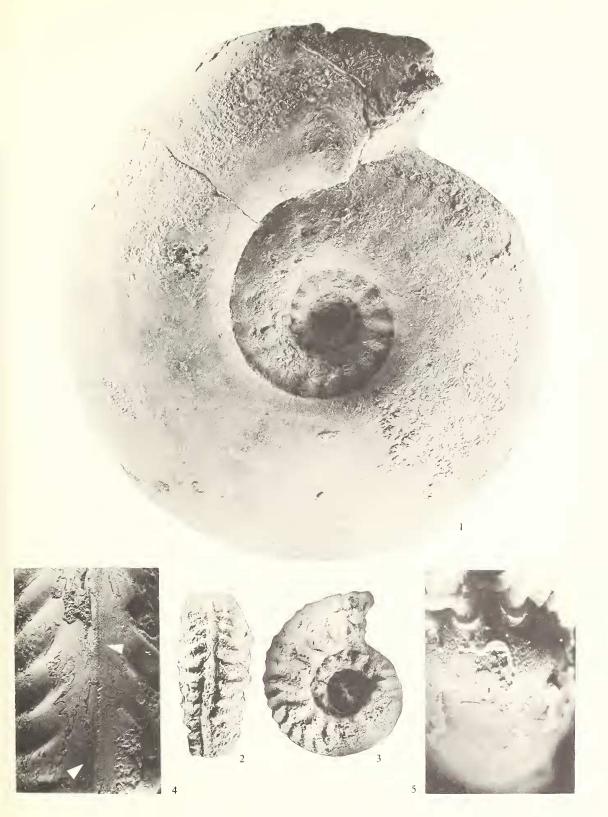
Bredyia subinsignis (Oppel) [M]

Fig. 1. A complete macroconch showing slight constriction of the aperture on the mature bodychamber. From Bed 22 (Scissum Bed) of Bonscombe Hill, near Shipton Gorge, Dorset. The reverse half of the specimen was eroded before subsequent deposition of Bajocian (Garantiana Zone) sediments. BM C78467 (author's collection), ×0·5.

Figs. 2, 3. A septate nucleus from the Scissum Bed of Bradford Abbas, Dorset. BM C77992 (Buckman Collection), ×1.

Fig. 4. The impression of ventral siphuncular attachment scars on the holotype of *Bredyia crassornata* (Buckman), as c. 114 mm diameter. MM L11221 (Buckman Collection), $\times 1.5$.

Fig. 5. Dorsal wrinkle layer at 7·12 mm diameter on the specimen BM C78465 (author's collection), locality and horizon as fig. 1, \times 8·6.



SENIOR, Bredyia from the Jurassic of Dorset

Bredyia subinsignis (Oppel, 1856)

- *1856 Ammonites subinsignis; Oppel, p. 367 [M].
- ?1874 Ammonites alleoni; Dumortier, p. 259, pl. 52, figs. 3, 4 [M].
- ?1874 Ammonites subinsignis Oppel; Dumortier, p. 261, pl. 53, figs. 1, 2 [M].
- v. 1883 Harpoceras insigne Schübler; Wright, p. 453, pl. LXXV, figs. 1-3 [M].
 - ?1892 Hammatoceras newtoni; Buckman, p. 259.
 - 1893 Ammonites feugeurollense; Brasil, p. 39, pl. 5, figs. 1, 2 [M].
 - 1904 Hammatoceras dumortieri; Prinz, p. 74.
 - 1905 Hammatoceras subinsignis (Oppel); Benecke, p. 331, pl. XXXII, fig. 2 [M].
- v. 1910a Burtonia crassornata; Buckman, p. 97, pl. 9, fig. 1; pl. 10, fig. 1 [M].
 - 1910b Bredyia crassornata (Buckman); p. xciv [M].
- v. 1925 Bredyia crassornata (Buckman), pl. DLXXVII [M].
 - 1925 Hammatoceras subinsignis (Oppel); Renz, pl. 10; pl. 1, fig. 5 [M].
 - 1962 Hammatoceras alleoni Dumortier; Migacheva, p. 82, pl. 8, figs. 1, 3 [M].
 - 1962 Hammatoceras subinsignis Oppel; Migacheva, p. 82, pl. 8, fig. 8 [M].
 - 1963 Pseudammatoceras subinsignis (Oppel); Elmi, p. 13, pl. I, figs. 1, 2 [M].
 - ?1963 Parammatoceras alleoni (Dumortier); Elmi, p. 55, pl. VIII, fig. 1.
 - 1963 Parammatoceras suballeoni Elmi; p. 57, pl. VIII, fig. 4 [M].
 - 1963 Pseudammatoceras feugeurollense (Brasil); Elmi, p. 93 [M].
 - 1964 Bredyia newtoni (Buckman); Westermann, p. 359 [m].

Type material. Although described in 1856 by Oppel, this species was not figured until 1925 when Renz redescribed it in an attempt to stabilize the species. The specimen Renz figured (1925, pl. 1, fig. 5) is the only remaining example in Oppel's Collection (Dr. G. Schairer in litt) and is here selected as lectotype of the species. The lectotype is from the Torulosus Schichten (= Opalinum Zone) of Gomaringen, Württemberg, South West Germany and is deposited in the University Palaeontological Collection, Munich (MU ASV11176).

Diagnosis. As for the genus.

Stratigraphical and geographical distribution. As for the genus.

Other material. During this study 76 examples of this species were examined (42 macroconchs and 34 microconchs), all are from English sources, unless otherwise stated.

OPALINUM ZONE

Macroconchs. Burton Cliff, Burton Bradstock, Dorset, bed 8a of Richardson (1928, p. 63), BM C78456 (author's coll.), B 1902, B 2078, B 4164, B 4596, B 7476. Haresfield Hill, Gloucestershire, BM C9216 (S. Buckman Coll.), OUM J16218; Frocester Hill, near Stroud, Gloucestershire, BM 67903 (Etheridge Coll.). La Verpilliere, Isère, France, LY 9110 (holotype of Ammonites alleoni, Dumortier Coll.).

Microconchs. BM C77972-77975, BM C77977, BM C77982-77983 (Buckman Coll.), B 2079, B 2139, B 4580. Sandstone below Scissum Bed, Green Hill, Innesacre Farm, near Bridport, Dorset, BM C78463 (author's coll.).

SCISSUM ZONE

Macroconchs. Burton Bradstock (probably Burton Cliff), Dorset, MM L1121 and GSM 47763 (holotype and paratype of Bredyia crassornata, Buckman Coll.), GSM 72799 (Spath Coll.), BM 50642 (Morris Coll.), BM C10242 (Witchell Coll.), BM C77958 (Buckman Coll.).

Scissum Bed (bed 7 of Richardson 1928, p. 63), Burton Cliff, Burton Bradstock, B 1885, B 3592, B 6057; BM C78462 (author's coll.). Quarry Hill, Chideock, OUM J33812 (Walford Coll.). Bed 22 Bonscombe Hill, near Shipton Gorge, BM C78465-78467 (author's coll., mentioned Senior *et al.* 1970, p. 116). Stony Head, Loders Cross, near Bridport, B 4856. Quarry north-east of Loders Cross (bed 2 of Bomford 1948, p. 148), near Bridport, B 2474-2475, SH 55104 (Bomford Coll.), GSM ZK1401-1402 (Bomford Coll.). Gribbs Quarry, Vinney ('Vetney') Cross, near Bridport, BM C77989 (S. Buckman Coll.). Upton Farm section, Matravers, near Bridport, GSM 72800-72801 (Spath Coll.), BM C78468 (author's coll.), bed 2 of the same locality (mentioned Senior *et al.* 1970, p. 118). Broad Windsor, GSM 3307 (Sharpe Coll.). Bradford Abbas, BM C77991-77992 (Buckman Coll.). Marston Road Quarry, near Sherborne, BM C77990 (Buckman Coll.). Crewkerne Station Quarry (more probably the Crewkerne Railway

Cutting), BM C77993 (Buckman Coll.). Hampton, Somerset, BM C6218 (Slatter Coll.). Newmarket, Nailsworth, Gloucestershire, GSM 22813 (Lycett Coll.). Ravensgate Hill, near Cheltenham, GSM 25101 (Lycett Coll.). Leckhampton, near Cheltenham, GSM Y3444 (Hudleston Coll.). Oatley ('Otley') Hill, near Hook Norton, Oxfordshire, GSM Z3881 (Richardson Coll.), OUM J33628–33630 (Beesley Coll.), OUM J33646, Whichford Hill, near Hook Norton, OUM J33647 (Walford Coll.). Duston, near Northampton, GSM Y3345 (Hudleston Coll.), BM C77513. Billing Road, near Northampton, BM C77515.

Microconchs. Burton Cliff, Dorset (Scissum Bed, bed 7 of Richardson 1928, p. 63), BM C78457-78458, BM C78461, BM C78469-78460; BM C78462 (author's coll.); BM C77969-77970, BM C77981, BM C77997, GSM 3666 (Buckman Coll.); B 4563, B 6062. Scissum Bed, Green Hill, Innesacre Farm, near Bridport, BM C78463 (author's coll.) Sherborne (?Sandford Lane), GSM 69945 (S. Buckman, ex. J. Buckman Coll.); near Stroud, Gloucestershire, BM C10233 (Witchell Coll.); Wedford, BM C10333 (Witchell Coll.); Duston, near Northampton, GSM Y3346-3347 (Hudleston Coll.); GSM 1160 HW (Woodward Coll.); New Duston, near Northampton, BM C77994-779945 (Buckman Coll.); and Gayton, near Northampton, GSM h378 (Judd Coll.).

Description. Protoconchs in both forms are smooth and globular (dimension given in text-fig. 5), but none shows any apparatus other than a subcircular caecal bulb. Shallow nepionic constrictions occur approximately one whorl forward of the proseptum (between 0.80 and 1.09 mm diameter in the sample seen) and these have the form of a shallow sigmoidal groove on the internal mould (text-fig. 2). After the nepionic constriction the second growth stage occurs (cf. Currie 1944, pp. 192–194) and is marked by the formation of rounded whorl sections by 6 mm diameter in the macroconch and slightly earlier in the microconch. Early development of a subquadrate whorl profile in the microconch coincides with the first appearance of the ribbed ornament and a small keel (text-fig. 5). Although ribbing and the keel appear later in the ontogeny of the macroconch by 10 mm diameter both have very similar subquadrate whorl sections (text-fig. 2n, s). With increasing diameter the macroconch whorl profile progressively changes due to slight ventro-lateral compression and

	MACRO CONCH	MICROCONCH		
Protoconch dimensions (in millimetres)	m 0.500 diameter m 0.536 width (2)	m 0.380 diameter m 0,540 width (4)		
Position of nepionic constriction	170° after prosuture	180°-190° after prosuture		
Diameter at which the nepionic constriction occurs	1.08 mm.	0,80 - 1.09 mm.		
First appearance of ribbed ornament	5-6mm, diameter	4 -5mm, diameter		
Range of mature phragmocone diameters	c 164 - 203 mm.	c 2 3 - 27mm,		
Mean mature conch diameters	m 243.37mm.	m 37,96mm.		
Shell volutions	c 7.5	c 4.5 - 5		
Bodychamber length in all growth stages seen	m 221.5°	m 215.9°		

TEXT-FIG. 5. A comparison of macroconch and microconch data in *Bredyia subinsignis* (Oppel).

increasing prominence of the coarse-ribbed ornament. The resulting subtriangular or subquadrate sections are retained throughout the juvenile stage, up to about 90 mm diameter (Pl. 84, figs. 3, 4 and text-fig. 2b), after which a mature macroconch growth stage can be recognized when the whorl section becomes slightly inflated and fastigate with only a small keel (text-fig. 2a-e).

Although subquadrate whorl sections appear earlier in the microconch (at about 5 mm diameter) little further development of the whorl shape occurs and except for moderate increases in dimensions the profile remains the same up to the mature aperture. This profile is also accentuated by the early development of coarse falcoid ribbing which is tuberculate or nodate where the ribs bifurcate on the lower lateral portion of the whorl flanks (Pl. 84, figs. 9, 13). This strong ornament is supplemented throughout growth by fine falcoid growth lines. Nodate or tuberculate ribbing with growth lines is also a prominent feature of the macroconch (Pl. 83, figs. 1, 6) and may give an angular appearance to the whorl section (text-fig. 2e). After about 90 mm diameter, however, the ribbing gradually fades finally leaving the mature bodychamber ornamented only by surface lirae (Pl. 82, fig. 1). Each form of *Bredyia subinsignis* has almost the same number of ribs per whorl, varying with the ontogeny from 5 to 28, although the average for both forms is slightly different, microconch 17·34 per whorl (42 in sample), microconch 18·72 per whorl (34 in sample).

Both sexes in *subinsignis* show the usual features indicative of maturity. Changes in ornament and slight inflation of the fastigate whorl section after about 90 mm diameter in the macroconch are also accompanied by uncoiling of the umbilical seam (Pl. 81, fig. 4; Pl. 82, fig. 1); this occurs about one complete whorl (360°) before the mature aperture which is simple, falcoid, and collared (Pl. 82, fig. 1). Features indicative of maturity in the microconch are not as prominent. Ornamentation remains virtually the same until the final aperture and growth is almost linear, although the microconch is generally more evolute than the macroconch (compare Pl. 84, figs. 6, 9). The mature aperture is distinctive with the development of midlateral lappets and a small rostrum (Pl. 84, figs. 22, 24). The umbilicus in both forms is fairly large with small steep walls and is distinctly ornamented by the ribbing of previous immature whorls. All complete examples seen had half to three-quarters of a whorl of bodychamber (Pl. 82, fig. 1 and Pl. 83, fig. 1).

During dissection of the material the complete sutural ontogeny of each form was recorded at half whorl intervals and is represented in text-fig. 6. The retraction of the umbilical lobe attributed to this genus by Buckman (1910a, p. 97) and later reiterated

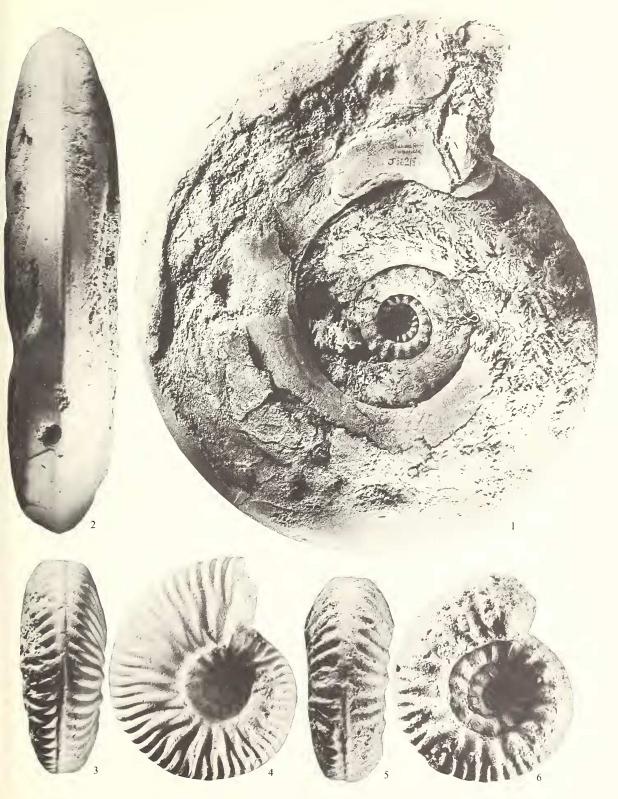
EXPLANATION OF PLATE 83

Bredyia subinsignis (Oppel) [M]

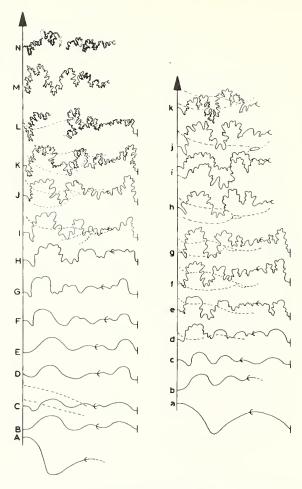
Figs. 1, 2. A mature and almost complete macroconch from the Cotswold Sands (Opalinum Zone) of Haresfield Hill, Gloucestershire. OUM J16218, ×0·5.

Figs. 3, 4. The plastotype of *Ammonites alleoni* Dumortier (LY 9110), from the Opalinum Zone (?) of La Verpilliere, Isère, France. Figured by Dumortier (1874, pl. 52, figs. 3, 4), ×1.

Figs. 5, 6. An unusual evolute immature macroconch from the Scissum Bed of Bradford Abbas, Dorset. BM C7791 (Buckman Collection), ×1.



SENIOR, Bredyia from the Jurassic of Dorset

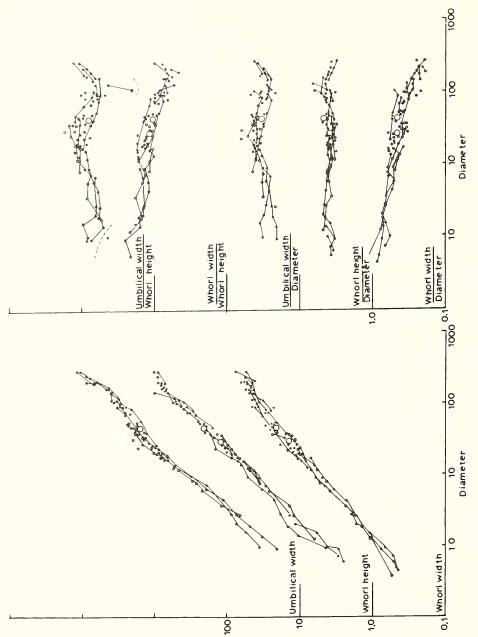


TEXT-FIG. 6. The sutural ontogeny of Bredyia subinsignis (Oppel). A-L, macroconch (BM C78465), from Bonscombe Hill, near Shipton Gorge, Dorset. A, prosuture at 0.48 mm diameter (\times 50). B, first suture at 0.50 mm diameter (\times 35). c, suture and nepionic constriction at 1.08 mm diameter (\times 35). D, 1.56 mm diameter ($\times 22.5$). E, 2.88 mm diameter ($\times 15$). F, 2.84 mm diameter $(\times 11)$. G, 5·23 mm diameter $(\times 10)$. H, 7·12 mm diameter $(\times 5)$. I, 13·14 mm diameter ($\times 3.75$). J, 17.17 mm diameter ($\times 2.3$). K, 47.8 mm diameter ($\times 0.7$). L, 92.7 mm diameter (\times 0.4). M, the paratype of B. crassornata (S. Buckman), from Burton Bradstock, Dorset (GSM 47763). Suture at c. 110 mm diameter $(\times 0.25)$. N, BM C78467, same locality and horizon as A-L. Suture at c. 203 mm diameter ($\times 0.2$). a-g, BM C78463, microconch, from Green Hill, Innesacre Farm, near Bridport, Dorset. a, prosuture at 0.40 mm diameter ($\times 35$). b, 1.36 mm diameter (\times 25). c, 2.80 mm diameter (\times 21.5). d, 3.84 mm diameter $(\times 6.25)$. e, 6.30 mm diameter $(\times 3.25)$. f, 6.3 mm diameter $(\times 1.9)$. g, 27.9 mm diameter (×1·7). h, BM C77515, macroconch from Billing Road, near Northampton, suture at 35 mm diameter ($\times 2.5$). i-k, microconchs from Burton Cliff, Dorset. i, GSM 3666, final approximated sutures at c. 25 mm diameter. j, BM C78457, suture at c. 26 mm diameter and k, BM C77997, suture at c. 23 mm diameter. All \times 2.5.

by Arkell (1957, p. L267) was not found to be noticeable. The sutural ontogeny of both sexes are very similar, especially in the early juvenile stages (text-fig. 6) although in late stages the development of the sutures in the much larger macroconch is naturally more pronounced. However, the relative simplicity of the macroconch sutures, even at the maximum of their development (about 90 mm diameter), is unusual and unlike that seen in other hammatoceratinids (text-fig. 3d, f). The crowding and simplification of the final sutures in the mature examples of both sexes is a common feature in most mesozoic ammonites (text-fig. 6). Dorsal wrinkle-layer structures were seen at various dimensions on both forms (Pl. 82, fig. 5) and showed great similarity with those described in the Graphoceratidae (Senior 1971). Siphuncular attachment scars sited parallel to the siphuncle tube, described by Neaverson (1927) and Hölder (1973, p. 44) were also seen (Pl. 82, fig. 4).

Dimorphism. There can be little doubt that the two forms of Bredyia described above are conspecific dimorphs, especially since they are found in the same strata with Erycites being the only other hammatoceratinid present. The large differences in dimensions, especially in diameter, are a function of sexual dissimilarity only. The macroconch: microconch size ratio (6·4:1) may be misleading, as the full size range of mature individuals (especially of the microconch) is uncertain due to a shortage of suitable material. It is, however, similar to the same ratio seen in Toarcian hammatoceratinids (Dr. M. K. Howarth pers. comm.). Certainly the initial growth of both forms is almost identical, having protoconchs of similar shape and size (text-fig. 5), equivalent placings of the nepionic constriction, and rapid development of rounded, then robust angular whorl sections (text-fig. 2).

Graphical representation of the biometric data obtained from both forms also shows an identical relationship up to about 27 mm diameter (text-fig. 7). A direct comparison can be made between the microconch and macroconch with the whorl width/whorl height ratio; in the microconch the value of this ratio remains at above 1.00 throughout development, whereas in the macroconch, this value drops appreciably below 1.00 with the onset of maturity, after about 90 mm diameter. This change of ratio can also be correlated in the macroconch with the loss of the ribbed ornament and marked uncoiling of the umbilical seam. Similar parallel developments can be seen in other plotted ratios (text-fig. 7). Up to diameters of 27 mm there is very little to separate the sutural ontogeny of either form (text-fig. 6), although the sutures of the macroconch become more complex at a later stage, a function of the enormous difference in size (text-fig. 6K-N). The skeletal development of the second lateral saddle in the macroconch (text-fig. 6L) is of interest; this feature is not always visible in every specimen, as the acme of development seems to be reached at about 90 mm diameter and subsequent sutures become more simplified (text-fig. 6M-P). This skeletal appearance is common to most hammatoceratinids (text-fig. 3) and also the sonniniids, but the invariable absence of this feature at larger diameters makes it sometimes very difficult to distinguish the macroconch of B. subinsignis from that of Ludwigia haugi Douvillé, the general morphology and sutural pattern being similar. This has possibly been one cause of misidentification, particularly the records of Bredyia from the Murchisonae Zone. Using the complete ontogeny of each macroconch one can readily distinguish between both species.



TEXT-FIG. 7. Graphical representation of the ontogeny of *Bredyia subinsignis* (Oppel), • macroconch, o microconch, o the lectotype of *Ammonites subinsignis* Oppel. Both axes are logarithmic and each plotted parameter or ratio on the vertical axis is offset by one cycle.

So far only two other groups of microconchs, *Kialagvikes* and *Rhodaniceras*, have been recognized in the hammatoceratinid ammonites. The subgenus *Kialagvikes* was described by Westermann (1964, p. 391) from a large sample of ammonites obtained from Wide Bay, Alaska and there are general similarities in size and appearance between *Bredyia* [m] and *Kialagvikes*, yet the general lack of nodate or tuberculate ornament (with the exception of *K. spinosa*) and the minute keel in the latter makes it distinctive, as does the more complex sutural appearance. The presence of identical lappets and a small rostrum in both microconchs is probably only a general characteristic of the subfamily Hammatoceratinae.

Westermann (1964, p. 392) drew attention to the fact that the macroconch subgenus *Erycitoides* is always associated with *Kialagvikes* and he assumed that they have a dimorphic relationship. As Westermann also noted hammatoceratinid microconchs bear a strong resemblance to certain microconch Graphoceratidae. However, consideration of the whole ontogeny allows discrimination. Bearing in mind this similarity between the microconchs of these subfamilies, it is unfortunate that Elmi (1963, p. 60) failed to illustrate the sutures of the microconch *Rhodaniceras* although he writes 'La ligne cloisonnaire apparient au "type hammatoceratidien" . . .', but it is not unreasonable that *Rhodaniceras* is the microconch form of *Eudmetoceras*, as indicated by Elmi (1963, p. 61).

Discussion. One of the main problems involved in the understanding of this species, was the interpretation of the five trivial names available. In 1856 Oppel described a number of hammatoceratinids as Ammonites subinsignis, and because he never illustrated these some confusion resulted when later workers applied his nomenclature. The lectotype of this species is indifferently preserved, having a slightly contorted bodychamber (three-quarters of a whorl in length) with an entirely crushed and largely absent phragmocone (Pl. 84, figs. 3, 4). The appearance of the whorl section and level of ribbed ornament development indicate this as an immature specimen. I examined a plaster cast of the specimen figured by Renz (1925, pl. 1, fig. 5), and there is little doubt that this immature example is comparable with the better-preserved ammonites later described by Buckman (1910a, p. 97) as Burtonia crassornata Buckman. This comparison is also endorsed by Oppel's own account of the species (1856, p. 368) in which he recorded having found another example at Burton Bradstock, Dorset, the type area for crassornata. Before his description of Bredyia crassornata, Buckman (1892, p. 259) gave a very brief account of a small new hammatoceratinid from the Inferior Oolite of Northamptonshire. To this species Buckman gave the name Hammatoceras newtoni, but he failed to describe or figure this species adequately, even at a later date. It is difficult to recognize this species from Buckman's description and no type material seems to be available, although the specimen figured by Wright (1883, pl. LXXV, figs. 1-3) is probably the one seen by Buckman and therefore should be regarded as the lectotype of newtoni. This species has often been quoted in the literature, especially from the Scissum Zone, but the interpretation of it has varied, the name having been used for immature or nucleii specimens of the macroconch B. crassornata (= B. subinsignis) (e.g. Donovan 1954, p. 49) or for microconch hammatoceratinids (Westermann 1964, p. 359). Although the former interpretation is probably correct, there is a considerable degree of uncertainty attached to the use of this name. Two ammonites found at Feuguerolles-Sur-Orne and figured by Brasil (1893, pl. 5, figs. 1, 2) as H. feugeurollense would also seem to be synonymous with subinsignis, but regrettably these specimens were destroyed in air raids on Caen in 1944. This hammatoceratid apparently only occurs rarely in the Opalinum Zone of the Normandy region (Dr. N. Rioutt in litt.). In his classic work on the Jurassic palaeontology of the Rhône Basin, Dumortier (1874) figured several macroconchs which are possibly either synonymous with or closely related to B. subinsignis (Oppel). In the former category are A. alleoni Dumortier (1874, pl. LII, figs. 3, 4) and A. subinsignis Oppel (1874, pl. LIII, figs. 1-4), later redescribed by Prinz (1904, p. 74) as H. dumortieri. Determining the stratigraphical horizon of Dumortier's specimens is difficult because he cited all the material as having come from the 'Zone de l'Ammonites Opalinus', which encompasses not only the whole of the Aalenian but also the upper portion of the Toarcian. Elmi (1963) investigated the stratigraphical position

of Dumortier's material and concluded that *alleoni* possibly came from the Murchisonae Zone and *dumortieri* originated very doubtfully from the Opalinum Zone (the horizon of origin being highly condensed, from Upper Toarcian–Lower Aalenian).

Conclusions. A specimen from Oppel's original collection figured by Renz (1925) is cited as the lectotype of *B. subinsignis* (Oppel). The type species of *Bredyia*, *Burtonia crassornata* Buckman (1910a) is considered a junior synonym of Oppel's species as are *H. newtoni* Buckman (1892), *H. feugeurollense* Brasil (1893) and several species described and figured by Dumortier (1874); notably *A. alleoni* and *A. subinsignis* (= *H. dumortieri* Prinz, 1904). The synonymy of *Bredyia* with *Hammatoceras* suggested by Géczy (1966, p. 30) is not upheld as considerable morphological differences indicate a separate generic status and *Pseudammatoceras* Elmi (1963), a genus also based on *A. subinsignis* Oppel, is considered a junior synonym of *Bredyia*.

The stratigraphical range of *B. subinsignis* seems to be limited to the Lower Aalenian (Opalinum and Scissum Zones) and records of its occurrence in the Murchisonae Zone have not been substantiated during this study. Geographically this uncommon ammonite seems to have been widely distributed throughout boreal Jurassic seas in Europe and in Tethyan sediments of Caucasia and the Northern Mediterranean.

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EXPLANATION OF PLATE 84

Bredyia subinsignis (Oppel) [M]

Figs. 1, 2. A partial internal mould of an immature macroconch from the Northampton Ironstones of Duston, near Northampton. BM C77513, \times 1.

Figs. 3, 4. The plastotype of *Ammonites subinsignis* (Munich ASVIII 76), from the Torulosus Schichten (Opalinum Zone) of Gomaringen, near Tübingen, West Germany. Described by Oppel (1856, p. 367) and later figured by Renz (1925, pl. 1, fig. 5), ×1.

Figs. 5, 6. An ironstone internal mould of a septate nucleus from Billing Road, near Northampton. BM C77515, \times 1.

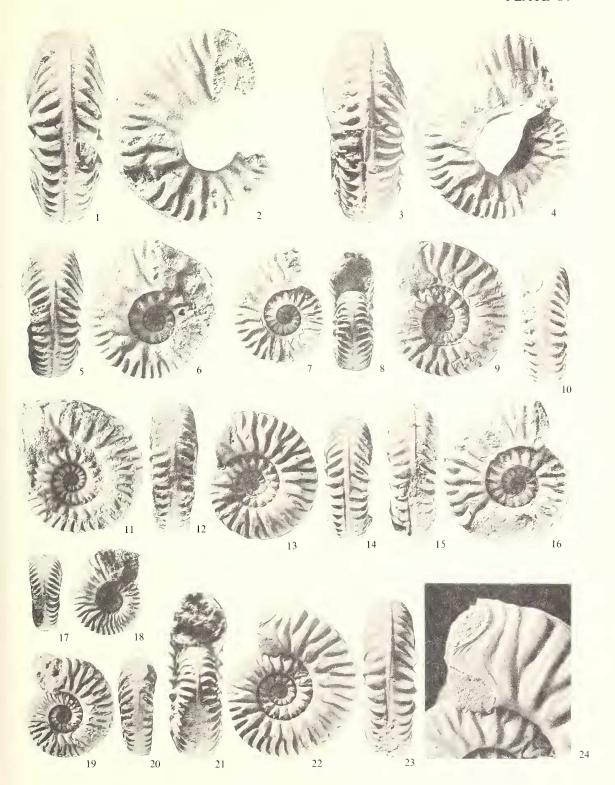
Bredyia subinsignis (Oppel) [m]

Figs. 7, 8. A complete but immature example from the Scissum Bed of Sherborne (probably Sandford Lane), Dorset. GSM 69945 (Buckman Collection), ×1.

Figs. 9, 10. A mature specimen showing the base of lappets from the Scissum Beds (Scissum Zone) of Burton Cliff, Dorset. GSM 3666 (Buckman Collection), ×1.

Figs. 11, 12. A mature example with a broken mouth border from the Northampton Sands of New Duston, near Northampton. BM C77995 (Buckman Collection), ×1.

Figs. 13–24. Microconchs from the Scissum Beds of Burton Cliff, Dorset. 13, 14, a mature specimen with an incomplete aperture (BM C77997, Buckman Collection). 15, 16, another incomplete but adult example (BM C77985, Buckman Collection). 17, 18, and 19, 20 (BM C78460 and BM C78458 respectively, both author's collection), complete immature specimens. 21–24, a well-preserved adult showing very fine midlateral lappets and small rostrum (BM C78457, author's collection). All ×1, with the exception of fig. 24 which is ×3.



SENIOR, Bredyia subinsignis

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